

# Role of Reproductive Diapause in the Adaption of the Tarnished Plant Bug (Heteroptera: Miridae) to Its Winter Habitat in the Mississippi River Delta

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**ABSTRACT** Reproductive diapause in the tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois), was studied by dissection of field collected adults or adults reared from field collected nymphs in 1999–2001 in Washington County near Stoneville, MS. The critical photoperiod for diapause induction was 12.5:11.5 (L:D) h, or  $\approx$ 12 September. This photoperiod was also near the day-length at which new generation adults produced in late winter and early spring became reproductive. Overwintering adults collected from winter host plants in December 1999 and 2001 began breaking diapause in the second and third weeks of December at a day-length near 10:14 (L:D) h. Most of the overwintering females collected on winter host plants had mature eggs by the end of December in both winters, and new generation adults were produced on winter hosts by the second or third week in March. Overwintering adults also were collected in January 2002 from plant debris not associated with any winter host plant. Most of the females overwintering in plant debris had mature eggs at the end of January, approximately 1 month later than overwintering females collected from winter hosts. This indicated that the adults from plant debris were in a different state of diapause, because they did not overwinter on a food source and matured reproductively at a later date. The winters of 1998–1999 and 1999–2000 were mild, whereas in the winter of 2000–2001, winter host plants were killed or stunted by cold weather. Diapause in plant debris in the winter of 2000–2001 was probably favored, because these adults would be more likely to survive until suitable host plants were available.

**KEY WORDS** tarnished plant bug, *Lygus lineolaris*, diapause, photoperiod

THE TARNISHED PLANT BUG, *Lygus lineolaris* (Palisot de Beauvois), is found in all agricultural regions of the United States and Canada, and in most states of Mexico (Kelton 1975). It has a very broad feeding niche, having been reported on 328 host plant species (Young 1986). It will also prey on or scavenge other arthropods. In the Mississippi River Delta region of Arkansas, Louisiana, and Mississippi, 169 host plant species have been reported, most of which are weeds (Snodgrass et al. 1984). In this region, cotton, *Gossypium hirsutum* L., is the main crop damaged by tarnished plant bugs, which are controlled almost exclusively with insecticides. In the midsouth they have become resistant to pyrethroid insecticides, and exhibit lower levels of resistance to a cyclodiene and several organophosphate insecticides (Hollingsworth et al. 1997, Pankey et al. 1996, Snodgrass and Elzen 1995, Snodgrass 1996). Once eradication of the boll weevil, *Anthonomus grandis* Boheman, has been completed in the midsouth, tarnished plant bugs could be one of the main pests of cotton. Boll weevil eradication programs and the use of transgenic Bt cotton for control of bollworm, *Helicoverpa zea* Boddie, and tobacco budworm, *Heliothis virescens* (F.), have greatly reduced insecticide use in cotton in this region. The

benefits of decreased grower costs and less environmental pollution derived from reduced insecticide input will be lessened if insecticides must be used for tarnished plant bug control. Alternative control methods for tarnished plant bugs are badly needed, and development of an integrated control program requires a thorough knowledge of their basic biology.

The tarnished plant bug overwinters as an adult in plant debris. Crosby and Leonard (1914) described the overwintering adults as being in a state of hibernation. Tarnished plant bug adults in the midsouth can be collected from wild hosts during every month of the year (Snodgrass et al. 1984). In the winter months of December–February, two species of wild host plants, shepherd's purse, *Capsella bursa-pastoris* (L.) Medicus, and henbit, *Lamium amplexicaule* L., are in bloom, especially in winters with average or above average temperatures. The presence of flower buds and blooms are important, since tarnished plant bugs use them as a preferred feeding sites (Snodgrass et al. 1984). Some overwintering tarnished plant bugs can be collected on these host plants, but some can also be collected from plant debris not associated with winter host plants (Cleveland 1982).

Despite its adaptive importance, diapause in the tarnished plant bug has only been investigated in the laboratory. Bariola (1969) studied diapause by rearing bugs at several different temperatures and photoperiods. He found that nymphs were the life stage that is sensitive to a diapause-inducing stimulus, and that newly hatched nymphs reared at 21°C and 27°C in photoperiod of 12.5:11.5 (L:D) h or less produced adults in diapause. Diapausing adults resulting from nymphs reared at 12:12 (L:D) h and 21°C became fully reproductive approximately 2 wk after exposure to photoperiods of 13.5:10.5 (L:D) h at 27°C. Newly hatched nymphs reared at 21°C and 27°C and 13:11 (L:D) h produced a mixture of reproductive and diapausing adults. Newly hatched nymphs that were reared at photoperiods of 13.5:10.5 (L:D) h or longer produced only reproductive adults.

The current study was conducted to obtain information on reproductive diapause in the tarnished plant bug in the Mississippi River Delta of the mid-south. This included determination of when diapause began and ended under field conditions and how reproductive diapause allowed tarnished plant bugs to adapt to their winter environment.

### Materials and Methods

#### Determination of Diapause in Field Populations.

All weather data were obtained from the Stoneville Weather Station, Delta Branch Research and Experiment Station, Stoneville, MS. A summary of weather data for Stoneville, presenting average data for 1964–1993, is found in Boykin et al. (1995), and 30-yr average weather data and day-length were taken from this publication. Plant bugs were collected with a sweep net from wild host plants near Stoneville or other areas in Washington County, MS, from August through April. Beginning in August of each year (1999–2001), nymphs were collected and reared to adults to determine reproductive status. These adults were dissected to determine their reproductive state at 7 d of age or older. The reproductive systems of nondiapausing adults of both sexes are completely developed by this age. Collections of nymphs were made at approximately weekly intervals. When nymphs became difficult to collect (in November and December), adults were collected and dissected on the same or following day. The main host plant from which collections were made in the summer and autumn were goldenrod (*Solidago altissima* L.), giant ragweed (*Ambrosia trifida* L.), pigweed (*Amaranthus* spp.), and horseweed (*Conyza canadensis* (L.) Cronquist). Collection hosts in the winter and early spring included henbit, shepherd's purse, sour dock (*Rumex crispus* L.), buttercup (*Ranunculus* spp.), daisy fleabane (*Erigeron philadelphicus* L.), and butterweed (*Senecio glabellus* Poirét). Adults were collected from dead plant debris using a sweep net in January and February 2002. The field where these adults were collected was out of agricultural production and had been replanted with several species of hardwood trees that were 0.9–1.5 m tall. The main tarnished plant bug

host plants present were giant ragweed, goldenrod, horseweed, and slender aster (*Aster exilis* Elliot). Dead plant tissue from several species of grass were also present throughout the field. No winter host plants were growing in the field when the adults were collected. Sweeps taken in the thickest debris often caught the highest numbers of bugs. This collection method was used only in 2002.

Nymphs were reared outside in 1999 in a screened enclosure with a roof, which provided protection from rain and partial shade during the day. Nymphs were placed in 4.6-liter cardboard containers, the tops and bottoms of which were composed of organdy cloth. Each container held up to 100 nymphs that were fed broccoli (*Brassica oleracea* L. variety *botrytis* L.). Food was changed every 2 d, and adults that had developed were removed. Adults were held in identical containers, however, green bean pods (*Phaseolus vulgaris* L.), were used as food. High humidity and temperatures associated with rearing the plant bugs outside in 1999 caused food spoilage and high nymphal mortality, which often exceeded 50%. In 2000 and 2001, nymphs and the resulting adults were reared indoors using a room maintained at  $25 \pm 4^\circ\text{C}$  and ambient relative humidity. The rearing containers were held on a table in front of a south-facing window to receive natural daylight. The room was also illuminated with overhead fluorescent lights from 0700 to 1530 on weekdays.

Failure of the reproductive organs to enlarge, and hypertrophy of the fat body were the criteria used to determine diapause (Lees 1955). The female reproductive system of *L. lineolaris* is described in Davis (1955). The male reproductive system of *L. lineolaris* has not been described, however, it is very similar to the male reproductive system of *Lygus hesperus* Knight (Strong et al. 1970). One difference between the species was that the testes of *L. lineolaris* had seven lobes instead of the five lobes described for *L. hesperus*. Tarnished plant bugs in the process of changing from the diapause state to a reproductive state were also found. Such adults, both male and female, still had large to moderately sized fat bodies with reproductive organs in different states of maturity. In a female, if the ovaries had one or more mature eggs (eggs in which the operculum was developed), or enlarged ovaries with developing oocytes, and or it had been recently mated [the genital pouch was greatly enlarged (Strong et al. 1970)], it was considered to be reproductive even though the fat body was enlarged. In males, it was often difficult to determine whether the testes had begun to enlarge because they were frequently covered by a membrane with a white layer of what appeared to be fat. If white fluid was visible in the accessory glands and seminal vesicle, and the accessory glands had begun to enlarge, a male was considered to be reproductive. Adults were killed and dissected in 70% alcohol.

**Utilization of Winter Host Plants.** Beginning in January and continuing through April of 1999–2002, winter and early spring wild host plants were sampled (as weather permitted) on a weekly basis with a sweep net to determine when nymphs were present and how

long it took for new generation adults to be produced. Nymphal instars were determined based on descriptions found in Crosby and Leonard (1914).

**Field Numbers of Eggs and Nymphs in Henbit.** A 3.7-ha field with a good stand of henbit located near Hollandale, MS, was sampled with a sweep net on 25 January 1999, and first-instar tarnished plant bugs were found. Plant density counts were taken on 26 January using a ring (0.56-m diameter) made from plastic-coated clothesline wire, which encompassed an area of 0.25 m<sup>2</sup>. The ring was placed at random at 30 locations across the field, and the number of henbit plants found within the ring were counted. The counts were used to calculate the average number of plants per ha. Randomly selected henbit plants were carefully cut at the soil line and placed individually into 10-liter plastic bags. In the laboratory, plants were cut into 8- to 10-cm sections and examined under magnification for tarnished plant bug eggs and nymphs. The bags were emptied of all plant material and examined for nymphs. Plant pieces containing eggs were held for egg hatch at 25°C and RH of  $\geq 70\%$ . The survey was repeated at weekly intervals through February. Ten plants were examined on 27 January and 3 February, whereas 20 plants were examined on 10, 17, and 23 February.

**Field Rate of Development on Henbit.** Because finding first-instar nymphs on henbit in January of 1999 was considered an unusual event, a test was conducted to determine whether tarnished plant bug nymphs could successfully develop on henbit at this time of the year, and to determine the time required for development. Three flowering henbit plants were transplanted into each of five plastic pots (2.2 liter). Organdy cloth was placed over the plants, and it was supported by four wooden dowels (0.5 cm in diameter and 30 cm in length) driven into the soil of the pot. The cloth was secured to the outside edge of the pot using double-sided carpet tape. On 1 February, 10 first-instar nymphs were placed in each pot. The nymphs hatched from eggs laid in green beans by overwintering adults. The cages were held outside under a shed where they were protected from rain but received sunlight most of the day. The cages were checked frequently in February to ensure that the plants had adequate water and were healthy. In March, they were checked daily for adult tarnished plant bugs. The number of adults produced and the time required for their development were recorded.

**Development of Nymphs During Winter and Early Spring.** Overwintering adults were collected in January 2002 from henbit and allowed to oviposit in green bean pods in the laboratory. Egg hatch began on 30 January and on 1 February, 150 first instars were placed into a 4.6-liter cardboard container, the top and bottom of which had been replaced with organdy cloth. Green bean pods were added for food, and the container of nymphs was placed outside under a shed where it was protected from rain. The green bean pods were replaced every 2–3 d, unless a freeze occurred the previous night, in which case they were changed immediately.

Nymphs were counted on 18 February and 14 March to determine mortality. Adults that developed in the cage were placed into new containers and were provided green bean pods for food. Containers with adults were also held outside under the shed until they were 10 d or more of age, at which time they were dissected to determine their reproductive status. Adults were held for 10 d instead of the 7-d period used in the laboratory, to ensure that the reproductive systems of the adults (which were developing at the colder outside temperatures) were developed.

In a subsequent test, newly emerged nymphs from eggs laid in green bean pods in the laboratory by overwintering adults in January, February, and March 2002, were reared indoors near a south-facing window using the same rearing room described previously. The nymphs were reared on broccoli in rearing containers, as described in Snodgrass and McWilliams (1992). Numbers of nymphs in each container varied from 20 to 100 depending on the number that hatched overnight. Containers of nymphs were set up on 1, 10, and 28 February; and on 11, 19, and 25 March. Food was changed every 2–3 d, and adults that developed were kept in identical containers and were provided green bean pods as food. Adults were dissected to determine their reproductive status when they were 7 d or older.

## Results

**Determination of Diapause in Field Populations.** The critical photoperiod for diapause induction [the point on a response curve in which 50% of the insects entered diapause (Tauber et al. 1986)] was approximately 12 September (a day-length of 12.5 h) in all 3 yr (Table 1). Very few adults ( $\leq 8\%$ ) were in diapause before 28 August in the study and most of the nymphs collected after 12 September produced adults in diapause. A mixture of reproductive and diapausing adults was reared from nymphs collected between 28 August and the first two weeks in September. The percentage of nymphs collected after 12 September that produced adults in diapause reached 100% once for males (first week of November 1999) and five times (all in 2000) for females.

Nymphs collected on 31 October through the third week of November 2001 produced an increasing percentage of adults that were reproductive (Table 1). The percentages of adults that were reproductive went from 20.9 and 5.9% for males and females, respectively, in the third week of October to 79.4 and 55.6% for males and females, respectively, in the third week of November. During this same period in the previous 2 yr, the percentages of males and females that were reproductive were 0–6% (10.1% for males in the third week of November 2000). In the fourth week of November, the percentages of the adults that were reproductive dropped to 27.9% for males and 3.5% for females. Nymphs were not collected and reared on or after the fourth week in November 2001, and the percentages in diapause presented are for adults collected from wild hosts.

Table 1. Occurrence of reproductive diapause in field-collected tarnished plant bugs

Date collected <sup>a,b,c</sup>	1999				2000				2001			
	M		F		M		F		M		F	
	n	% diap.	n	% diap.	n	% diap.	n	% diap.	n	% diap.	n	% diap.
Aug. 1–7	10	0	10	0	–	–	–	–	–	–	–	–
8–14	20	0	14	0	–	–	–	–	–	–	–	–
15–21	10	0	14	7.1	204	2.0	195	1.0	–	–	–	–
22–29	15	0	20	0	213	8.0	207	4.8	87	2.2	106	3.8
Sept. 1–7	16	6.3	13	15.4	106	28.3	135	23.7	59	42.4	56	14.3
8–14	24	40.5	31	48.4	105	51.4	125	34.4	86	63.9	80	48.8
15–21	15	86.7	30	86.7	138	84.8	96	85.4	93	87.1	98	73.5
22–29	50	98.0	52	98.1	114	98.2	109	100.0	129	79.1	135	94.1
Oct. 1–7	39	92.3	50	90.0	68	95.6	80	95.0	122	84.4	100	87.0
8–14	58	96.6	53	92.5	80	90.0	90	93.3	87	80.5	126	86.5
15–21	48	91.6	41	92.7	120	96.7	103	99.0	72	77.8	102	82.4
22–29	50	98.0	52	98.1	114	98.2	109	100.0	129	79.1	135	94.1
31	–	–	–	–	76	92.1	68	100.0	144	54.9	175	67.4
Nov. 1–7	96	100.0	114	95.3	–	–	–	–	–	–	–	–
8–14	54	94.4	50	98.0	251	92.4	248	97.2	134	50.0	146	56.2
15–21	50	96.0	50	94.0	99	89.9	101	100.0	180	20.6	198	44.4
22–29	54	92.6	59	93.2	157	85.4	106	100.0	122	72.1	113	96.5
30	–	–	–	–	–	–	–	–	120	80.0	88	98.9
Dec. 1–7	–	–	–	–	120	87.5	90	97.8	119	85.7	84	94.1
8–14	55	89.1	52	88.5	–	–	–	–	138	36.2	75	54.7
15–21	17	76.5	29	58.6	–	–	–	–	67	3.0	31	12.9
22–29	70	8.6	45	8.9	–	–	–	–	15	0.0	13	7.7
Jan. 8–14	–	–	–	–	46	2.2	26	7.7	–	–	–	–

Nymphs were reared outdoors or indoors near natural light and dissected as adults at  $\geq 7$  d of age.  
<sup>a</sup> Nymphs were reared in an outside enclosure in natural daylight and temperatures in 1999. In 2000 and 2001, they were reared indoors with fluorescent and natural daylight at  $25 \pm 4^\circ\text{C}$ .  
<sup>b</sup> Data shown for December 1999 and January 2000, and on or after 15 November 2000 and 22 November 2001, are from dissection of plant bugs collected as adults.  
<sup>c</sup> No adults were collected after the first week in December 2000 because of cold temperatures which killed or stunted winter host plants.

Termination of diapause began in 1999 during the third week of December, and in 2001 during the second week in December (Table 1). Day-length during this 2-wk period ranged from 9.9 to 10 h at Stoneville, MS. Adults could not be collected after the first week in December in 2000 because of a colder than normal winter, which stunted or killed the wild host plants. The average high temperature in December was  $7.2^\circ\text{C}$  compared with a 30-yr average of  $12.2^\circ\text{C}$  for December

at Stoneville. The average low temperature was  $-2.6^\circ\text{C}$  compared with a 30-yr average of  $2.3^\circ\text{C}$ . Temperatures in January and February of 2001 were normal; however, wild hosts did not get large enough to sample until mid February. Over 90% of the adults collected from wild hosts were reproductive by the last week of December in 1999 and 2001. Approximately 50% of the females found on wild hosts had mature eggs by mid December in 2001, and by 9 January all females contained mature eggs (Table 2). In contrast, only 28.3% of reproductive females collected on 14 January from plant debris had mature eggs (Table 3). By 4 February, all reproductive females from plant debris had mature eggs. Day-length during January through 4 February ranged from 10.0 to 10.7 h. These data showed that females that over-

Table 2. Reproductive state of tarnished plant bugs collected from winter host plants in Washington County, MS

Date collected <sup>a</sup>	n <sup>b</sup>	% Females reproductive	% Reproductive females with mature eggs <sup>c</sup>
8 Dec. 99	52	11.5	16.7
14 Dec. 01	75	45.3	20.6
17 Dec. 99	29	41.4	66.7
21 Dec. 01	31	87.1	63.0
22 Dec. 99	45	91.1	61.0
28 Dec. 99	13	92.3	83.3
9 Jan. 02	31	100.0	100.0
10 Jan. 00	26	92.3	91.7
15 Jan. 02	18	100.0	94.4
23 Jan. 02	26	96.2	96.0
30 Jan. 02	30	100.0	100.0
4 Feb. 02	12	100.0	91.7
12 Feb. 02	13	100.0	100.0

<sup>a</sup> The host plants were henbit and shepherd's purse.  
<sup>b</sup> Number of female plant bugs dissected to determine their reproductive status.  
<sup>c</sup> Eggs with a developed operculum.

Table 3. Reproductive state of tarnished plant bugs collected in 2002 from plant debris in Washington County, MS

Date collected	n <sup>a</sup>	% Females reproductive	% Reproductive females with mature eggs <sup>b</sup>
14 January	51	90.2	28.3
22 January	33	90.9	66.7
29 January	73	100.0	86.3
4 February	9	100.0	100.0
12 February	4	100.0	100.0

<sup>a</sup> Number of female plant bugs dissected to determine their reproductive status.  
<sup>b</sup> Eggs with a developed operculum.

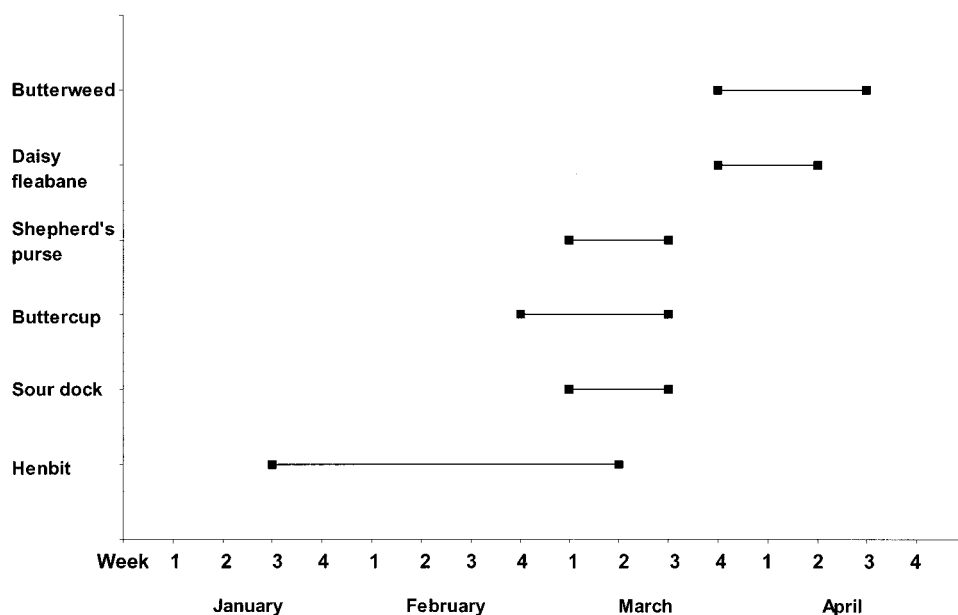


Fig. 1. Occurrence of nymphs on winter and early spring host plants from 1999 to 2001 in Washington County, MS. Each timeline begins with the earliest week in which nymphs were found and ends with the earliest week in which fifth instars were found.

wintered in plant debris produced mature eggs about four weeks later than the adults that remained active on wild hosts during the winter.

**Utilization of Winter Host Plants.** In 1999 and 2000, henbit was the earliest host plant on which tarnished plant bug nymphs were found in the sampled areas in Washington County (Fig. 1). Fifth-instar nymphs were present on henbit by 12 and 21 March in 1999 and 2000, respectively. This is not surprising, because henbit is consistently the first winter host to bloom, usually flowering by mid December. The presence of fifth instars was used as an indicator that successful completion of a generation occurred on a host plant species. The presence of new adults was not used, because new adults could have dispersed from other host species. The winter of 1999–2000 was not as warm as that of 1998–1999, but high and low temperatures were a little above the 30-yr average in December 1999 and January–March 2000. During the cold winter of 2000–2001, henbit was severely stunted and was not used by tarnished plant bugs as a reproductive host. Shepherd's purse also blooms in December during most years, but it is not as abundant as henbit, and is not a preferred reproductive host. In 1999 and 2000, nymphs were first found on shepherd's purse in early March with fifth instars present by the third or fourth week of March. Sour dock can bloom in late January; however, nymphs were not found on it until the first week of March 1999 and the second week of March 2000. Fifth instars were found on this host in early April 1999 and in the third week of March 2000. Nymphs were first found on buttercup in late February to early March with fifth instars present by the third or fourth week in March. The cold winter of 2000–2001 delayed the

growth of most of the winter hosts normally used by tarnished plant bugs for food and reproduction. The first nymphs were found in the fourth week of March and the first fifth instars in the second and third weeks in April 2001 on daisy fleabane and butterweed. Thus, in 2001, new generation adults were not present on the wild hosts sampled until the second and third weeks of April. In the milder winters of 1998–1999 and 1999–2000, new generation adults were present on wild hosts sampled by the second and third weeks of March, approximately 4 wk earlier than in 2000–2001.

**Field Numbers of Eggs and Nymphs in Henbit.** Two fifth-instar tarnished plant bug nymphs were collected when the field of henbit near Hollandale was sampled with a sweep net on 25 January 1999. These were overwintering nymphs, and were the only ones collected during this study. Nymphs have been reported to overwinter under mullien plant leaves in Illinois (Forbes 1884). The average density of the henbit plants in the field sampled for tarnished plant bug eggs and nymphs near Hollandale, MS was  $2.67 \pm 0.56$  (SEM) plants per  $0.25 \text{ m}^2$ , or 106,345 plants per ha. It required three people working approximately 8 h to examine 20 plants for eggs and nymphs. This limited the number of plants that could be sampled each week to 10 or 20. The highest number of eggs found were eight eggs in ten plants collected on 27 January. From 10 February through 23 February, the number of eggs found ranged from 5 to 7 per 20 plants, whereas the number of nymphs (mostly first or second instars) ranged from 1 to 5 per 20 plants. The sample size of 10 or 20 plants was most likely too small to accurately convert sample numbers to numbers of eggs or nymphs per ha. However, the number of eggs and



Table 4. Reproductive status of adult tarnished plant bugs that developed at different day lengths as nymphs

Nymphal developmental period <sup>a</sup>	Day length L:D h	Male		Female	
		n	% reproductive <sup>b</sup>	n	% reproductive
1 Feb.–27 Feb.	10.6:13.4; 11.4:12.6	12	33.3	7	0
10 Feb.–8 Mar.	10.9:13.1; 11.7:12.3	5	40.0	5	0
28 Feb.–23 Mar.	11.4:12.6; 12.2:11.8	29	79.3	32	18.8
11 Mar.–1 Apr.	11.8:12.2; 12.5:11.5	45	84.4	45	68.9
19 Mar.–12 Apr.	12.1:11.9; 12.9:11.1	8	100.0	18	88.9
25 Mar.–14 Apr.	12.3:11.7; 13.0:11.0	30	96.7	31	87.1
30 Mar.–19 Apr.	12.4:11.6; 13.1:10.9	22	100.0	14	92.8

<sup>a</sup> Nymphs and adults that developed when reared near a south-facing window in a room maintained at  $25 \pm 4^\circ\text{C}$ .

<sup>b</sup> Adults were dissected when  $\geq 7$  d to determine reproductive status.

nymphs found in only a few samples indicated that a substantial number of eggs and nymphs were present in the field. Two other types of hemipteran eggs were found in the henbit plants. These were eggs of nabids and insidious flower bugs, most likely *Orius insidiosus* (Say), both of which are important predators in crops grown in the midsouth. Numbers of nabid eggs found ranged from 5 to 18 in the samples, whereas a range of 1–12 *O. insidiosus* eggs were found in the samples. Identification of eggs of all three hemipterans were confirmed by holding them until hatch. Egg hatch in all three species was  $<50\%$  because of desiccation of the plant parts and/or fungal growth on the plant pieces. None of the predator nymphs were reared until adult, but adults of *O. insidiosus* were captured in sweep net samples taken in the field during February. The grower treated the sample field with an herbicide to kill the winter weeds during the third week of February, and the henbit was starting to die on 23 February when the last sample for eggs and nymphs was taken. The largest plant bug nymphs taken in henbit on this date were third instars.

**Field Rate of Development on Henbit.** For nymphs that were reared to adults on henbit, the average developmental time was  $41.4 \pm 0.73$  d (SEM). A total of 34 adults (68%) were obtained from the 50 first-instar nymphs that were used in this study. The temperatures during the winter of 1998–1999 were mild, and during December and March they were near the 30-yr average. Temperatures in January and February were above average. Beginning 17 January, the temperature did not drop below freezing until 14 February. During this period, the average high temperature was  $19.3^\circ\text{C}$ , whereas the average low temperature was  $8.3^\circ\text{C}$ .

**Development of Nymphs During Winter and Early Spring.** In the container of nymphs held outside during February and March of 2002, 127 (84.7%) of the nymphs were alive on 18 February, whereas 74 (49.3%) were alive on 14 March. Adults emerged beginning 19 March, and the last adult was found 25 March. Adults required 47–53 d to develop, and a total of 40 (18 males and 22 females) was obtained. All of the adults were in diapause when they were dissected.

Nymphs that were reared indoors produced females mostly in diapause when the day-length at which they developed began at 11.4:12.6 (L:D) h or

less (beginning dates of 1, 10, and 28 February) and extended through 12.2:11.8 (L:D) h or less (23 March) (Table 4). However, males developed a much higher percentage of reproductive adults (33.3–79.3%) at these day-lengths. Nymphal developmental periods that included a day-length of 12.5:11.5 (L:D) h or more (beginning dates of 11, 19, 25, and 30 March) produced mostly reproductive males and females.

## Discussion

In 1999, nymphs collected from wild hosts were reared under natural conditions of temperature and daylight, whereas in 2000 and 2001 nymphs were reared indoors using a mixture of fluorescent and natural light and a temperature of  $25 \pm 4^\circ\text{C}$ . The laboratory rearing removed the effect that naturally occurring changes in temperatures might have had. The percentages of plant bugs in diapause found each week in 1999 and 2000 were very similar (Table 1), suggesting that fluctuating temperatures had little effect on the induction of diapause. The percentages in diapause in 2001 was very similar to those of 1999 and 2000 through 25 October. The large increase in numbers of reproductive adults produced from nymphs collected and reared in late October and November of 2001 was unexpected and its cause is unknown. In the fourth week of November, and thereafter, the percentages of reproductive adults declined, because adults (not nymphs) were collected and these were from an adult population that included those previously produced in September and October. Warmer than normal weather during November and excellent growing conditions for autumn host plants may have been responsible for the increase. August had 21.36 cm of rain, which was 3.4-fold higher than the 30-yr average. Most of the autumn host plants of the tarnished plant bug are growing in August and benefited from the abundant rainfall in this hot month. Rainfall totals in September and October were a little above the 30-yr averages, whereas rainfall in November was 29.82 cm, which was 2.2-fold higher than the 30-yr average. The average high temperature in November was  $22.3^\circ\text{C}$  compared with the 30-yr average of  $17.6^\circ\text{C}$ . Bariola (1969) found that the induction and termination of diapause in the tarnished plant bug was influenced more by photoperiod than by temperature. However, a higher number of nymphs entered dia-

pause when reared at 21°C than at 27°C at day lengths of 12.5, 13.0, and 13.5 h.

Most of the nymphs collected and reared on 31 October and during the first three weeks of November were taken from pigweed at three locations in Washington County. Adults from nymphs that developed on other host plants at these times may or may not have produced as many reproductive adults because host plant species might influence diapause; however, the influence of host plant on diapause in the tarnished plant bug is unknown. Food can act as a major diapause regulating factor, mainly among insects with aestival diapause and tropical insects (Tauber et al. 1986). Hunter and McNeil (1997) found that larvae of the obliquebanded leafroller, *Choristoneura rosaceana* (Harris), that were fed chokecherry, *Prunus virginiana* L., were more likely to produce a second generation (not enter diapause) than were larvae fed three other host plant species. Larvae fed low-quality artificial diet were also more likely to enter diapause than those fed a high-quality diet. The quality of the wild hosts that developed under the excellent growing conditions (abundant water and higher than normal temperatures in November) in the autumn of 2001 may have been higher than in the previous 2 yr of the study and consequently, may have affected diapause.

The critical photoperiod for diapause induction was estimated to be 12.5 h (12 September), and was based on field collection and rearing of nymphs of different ages. Younger nymphs in each collection developed into adults at shorter day lengths than older nymphs collected on the same date. So, the percentage in diapause determined for adults reared from nymphs collected on the same date is an average for all ages of nymphs. Ideally, only first-instar nymphs would be collected and reared on each date, but this would be almost impossible to do in the field. Bariola (1969) concluded from his laboratory studies that the transitional day-length separating the induction or prevention of diapause was 13 h, because newly hatched nymphs reared at this day-length produced a mixture of diapausing and reproductive adults. This day-length occurred on 28 August at College Station, TX. Nymphs from his study that were reared at a photoperiod of 12.5:11.5 (L:D) h (12 September) should have entered diapause as adults. He predicted that all adults found in the field before 28 August should be reproductive, and all nymphs found after 12 September should enter diapause as adults. Nymphs completing development between 28 August and 12 September should be a mixture of reproductive and diapausing adults. His predictions were very similar to the findings in the current study. The day-lengths on 28 August and 12 September are the same in Stoneville, MS, and College Station, TX. Most adults that developed from nymphs collected before 28 August were reproductive, whereas nymphs collected after 12 September produced adults in diapause. A mixture of reproductive and diapausing adults developed from nymphs collected between 28 August and the first 2 wk in September. Beards and Strong (1966) estimated the

critical photoperiod for *L. hesperus* at Davis, CA, to be 13.5 h (20 August). *Lygus hesperus* began terminating diapause at Davis in November with  $\approx 50\%$  of the population reproductive by the middle of November. They thought that nymphs found in the field in late October and in November did not enter diapause. This is similar to what was found with the tarnished plant bug in 2001 of the current study. In late October and the first three weeks of November, a high percentage of the reared adults were reproductive. However, this did not occur in the previous two years, and *L. hesperus* breaks diapause a month earlier at Davis than the tarnished plant bug does at Stoneville.

The rapid increase in percentages of adults in diapause that occurred in September was typical of response curves found with long-day insects that enter diapause when exposed to shorter days of late summer and autumn (Tauber et al. 1986). Results from the current study do not show whether there was a difference in the intensity of diapause produced by the different day-lengths. In some insects, diapause-inducing day-lengths near the critical photoperiod produce a weaker (shorter) diapause than day-lengths well below the critical photoperiod (Tauber et al. 1986). In the current study, it may be that the tarnished plant bugs found to be active on winter hosts during December and January were those produced near the critical photoperiod of 12 September. These adults broke diapause during December, and females produced mature eggs approximately 4 wk earlier than adults found without food in plant debris in January. The adults found in plant debris were most likely in a more intense state of diapause and could have developed in October and November at shorter photoperiods. Both groups of adults broke diapause at photoperiods  $< 11$  h; however, it is not known what the diapause-terminating stimulus is for this species. For most temperate-zone species with an overwintering diapause, no specific diapause-terminating stimulus has been identified (Tauber et al. 1986).

Tarnished plant bugs completed their development on henbit in  $\approx 41.4$  d with good survival (34 of 50 first-instar nymphs became adults). This is important because henbit is the only abundant winter host plant that grows and blooms during mild to normal winters at Stoneville. Without this abundant host, reproductive activity in late December would not be advantageous. In the winter of 1998–1999 (Fig. 1), henbit allowed tarnished plant bugs to produce new generation adults by the second week of March. Sheperd's purse and buttercup also can be important as winter hosts, but are not nearly as abundant as henbit. The cold winter of 2001 stunted or killed winter host plants, preventing reproduction by tarnished plant bugs. The first new-generation adults were not produced until the second and third weeks of April, approximately 3 to 4 wk later than in the previous 2 yr. The part of the overwintering plant bug population in leaf litter that broke diapause in January 2002 most likely was less affected by the absence of host plants and better able to survive until hosts were available than those that overwintered on plants.

Although high mortality (73.3%) occurred in the nymphs reared outside in February and March 2002, the fact that 26.7% developed into adults showed that the nymphs were fairly tolerant of cold temperatures. The green bean pods in the container were frozen on several mornings, because there were 9 d in February in which the temperature dropped to  $\leq 0^{\circ}\text{C}$  with a low of  $-6.1^{\circ}\text{C}$ , whereas March had 10 d with temperatures of  $\leq 0^{\circ}\text{C}$  with a low of  $-7.2^{\circ}\text{C}$ . Nymphal populations on winter hosts would probably be affected more by a hard freeze that killed or damaged the winter host rather than by the cold itself. Little is known about the effect of freezing temperatures on tarnished plant bug eggs laid in winter hosts. Survival of eggs in late winter (February and March) is critical to *L. hesperus* at Davis, CA (Beards and Strong 1966). Overwintering adults are dead by mid February at Davis, and nymphs are not found until  $\approx 1$  April. Thus, *L. hesperus* passes late winter as eggs in host plants that require 4–6 wk to hatch. This is not the case for the tarnished plant bug in the midsouth where overwintering adults are present until mid April.

Henbit and a few other winter hosts that bloom in winter in the midsouth present the tarnished plant bug with an opportunity to reproduce at a time when competition from other phytophagous arthropods is greatly reduced. Predators such as nabids and insidious flower bugs were found to use the same winter host plants, so plant bugs reproducing in the winter may not escape predation. However, no parasitoid of tarnished plant bug nymphs is known to be active in the winter. Information from this study will be helpful in the development of cultural and biological control measures for plant bugs. It could also be used in the development of control measures such as mass release of sterile insects or treatment of host plants with an entomopathogen.

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### References Cited

- Bariola, L. A. 1969. The biology of the tarnished plant bug, *Lygus lineolaris* (Beauvois), and its nature of damage and control on cotton. Ph. D. Dissertation, Texas A&M University, College Station.
- Beards, G. W., and F. E. Strong. 1966. Photoperiod in relation to diapause in *Lygus hesperus* Knight. *Hilgardia* 37: 345–362.
- Boykin, D. L., R. R. Carle, C. D. Ranney, and R. Shanklin. 1995. Weather data summary for 1964–1993 at Stoneville, Mississippi. Tech. Bull. 201. Mississippi Agr. and For. Expt. Sta., Mississippi State, MS.
- Cleveland, T. C. 1982. Hibernation and host plant sequence studies of tarnished plant bugs, *Lygus lineolaris*, in the Mississippi Delta. *Environ. Entomol.* 11: 1049–1052.
- Crosby, C. R., and M. D. Leonard. 1914. The tarnished plant bug. *Cornell Agr. Expt. Stn. Bull.* 346: 463–525.
- Davis, N. T. 1955. Morphology of the female organs of reproduction in Miridae (Hemiptera). *Ann. Entomol. Soc. Am.* 48: 132–150.
- Forbes, S. A. 1884. Illinois State Entomologist Report. 13: 115–135.
- Hollingsworth, R. G., D. C. Steinkraus, and N. P. Tugwell. 1997. Responses of Arkansas populations of tarnished plant bugs (Heteroptera: Miridae) to insecticides, and tolerance differences between nymphs and adults. *J. Econ. Entomol.* 90: 21–26.
- Hunter, M. D., and J. N. McNeil. 1997. Host-plant quality influences diapause and voltinism in a polyphagous insect herbivore. *Ecology* 78: 977–986.
- Kelton, L. A. 1975. The lygus bugs (genus *Lygus* Hahn) of North America (Heteroptera: Miridae). *Entomol. Soc. Canada Mem.* 95: 1–101.
- Lees, A. D. 1955. The physiology of diapause in arthropods. Cambridge University Press, Cambridge, United Kingdom.
- Pankey, J. H., B. R. Leonard, J. B. Graves, and E. Burris. 1996. Toxicity of acephate, cypermethrin, and oxamyl to tarnished plant bugs in vial bioassays and cage studied on cotton, pp. 882–887. In D. J. Herber and D. A. Richter [eds.], *Proceedings, Beltwide Cotton Production Research Conference*, Nashville, TN. National Cotton Council, Memphis, TN.
- Snodgrass, G. L. 1996. Insecticide resistance in field populations of the tarnished plant bug (Heteroptera: Miridae) in cotton in the Mississippi Delta. *J. Econ. Entomol.* 89: 783–790.
- Snodgrass, G. L., and G. W. Elzen. 1995. Insecticide resistance in a tarnished plant bug population in the Mississippi Delta. *Southwest. Entomol.* 20: 317–323.
- Snodgrass, G. L., and J. M. McWilliams. 1992. Rearing the tarnished plant bug (Heteroptera: Miridae) using a tissue paper oviposition site. *J. Econ. Entomol.* 85: 1162–1166.
- Snodgrass, G. L., W. P. Scott, and J. W. Smith. 1984. Host plants and seasonal distribution of the tarnished plant bug (Hemiptera: Miridae) in the delta of Arkansas, Louisiana, and Mississippi. *Environ. Entomol.* 13: 110–116.
- Strong, F. E., J. A. Sheldahl, P. R. Hughes, and E.M.K. Hussein. 1970. Reproductive biology of *Lygus hesperus* Knight. *Hilgardia* 40: 105–147.
- Tauber, M. J., C. A. Tauber, and S. Masaki. 1986. Seasonal adaptations of insects. Oxford University Press, New York.
- Young, O. P. 1986. Host plants of the tarnished plant bug, *Lygus lineolaris* (Heteroptera: Miridae). *Ann. Entomol. Soc. Am.* 79: 747–762.

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